

TWO EARLY CRETACEOUS SPIRULID COLEOIDS OF THE NORTH-WESTERN CAUCASUS: THEIR SHELL ULTRASTRUCTURE AND EVOLUTIONARY IMPLICATIONS

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ABSTRACT. The rare phragmocone-bearing coleoids *Adygeya adygensis* gen. et sp. nov. and *Naefia kabanovi* sp. nov. are described from the Aptian of the north-western Caucasus (Russia). They are considered to be the earliest known members of the order Spirulida, belonging to two families, Adygeyidae fam. nov. and Groenlandibelidae, respectively. The siphuncular and shell wall ultrastructures of the coleoids were studied with SEM and compared with those of Recent *Spirula*.

The two coleoids under consideration possess a longiconic shell, a comparatively wide and strongly expanded siphuncle with spherulitic-prismatic connecting rings, a shell wall as thin as the septa, a short final chamber and comparatively long camerae. Both genera lack rostra and a nacreous layer in the shell wall. They differ mainly in the position of the siphuncle and the shape of septal necks.

Ultrastructural studies of the shell wall in *Adygeya*, *Naefia* and *Spirula* lead to the conclusions that in the lineage of Spirulida (1) the shell possesses the outer plate (*sensu* Appellöf 1893) instead of a rostrum, and (2) the shell wall lacks the nacreous layer. On the basis of the high stability of shell wall structure in cephalopod evolution, it is assumed that these structural differences indicate an early divergence of Decabanchia and Belemnioidea, and that the taxa which had a rostrum and a nacreous layer in the shell wall can hardly be interpreted as precursors of the Spirulida lineage.

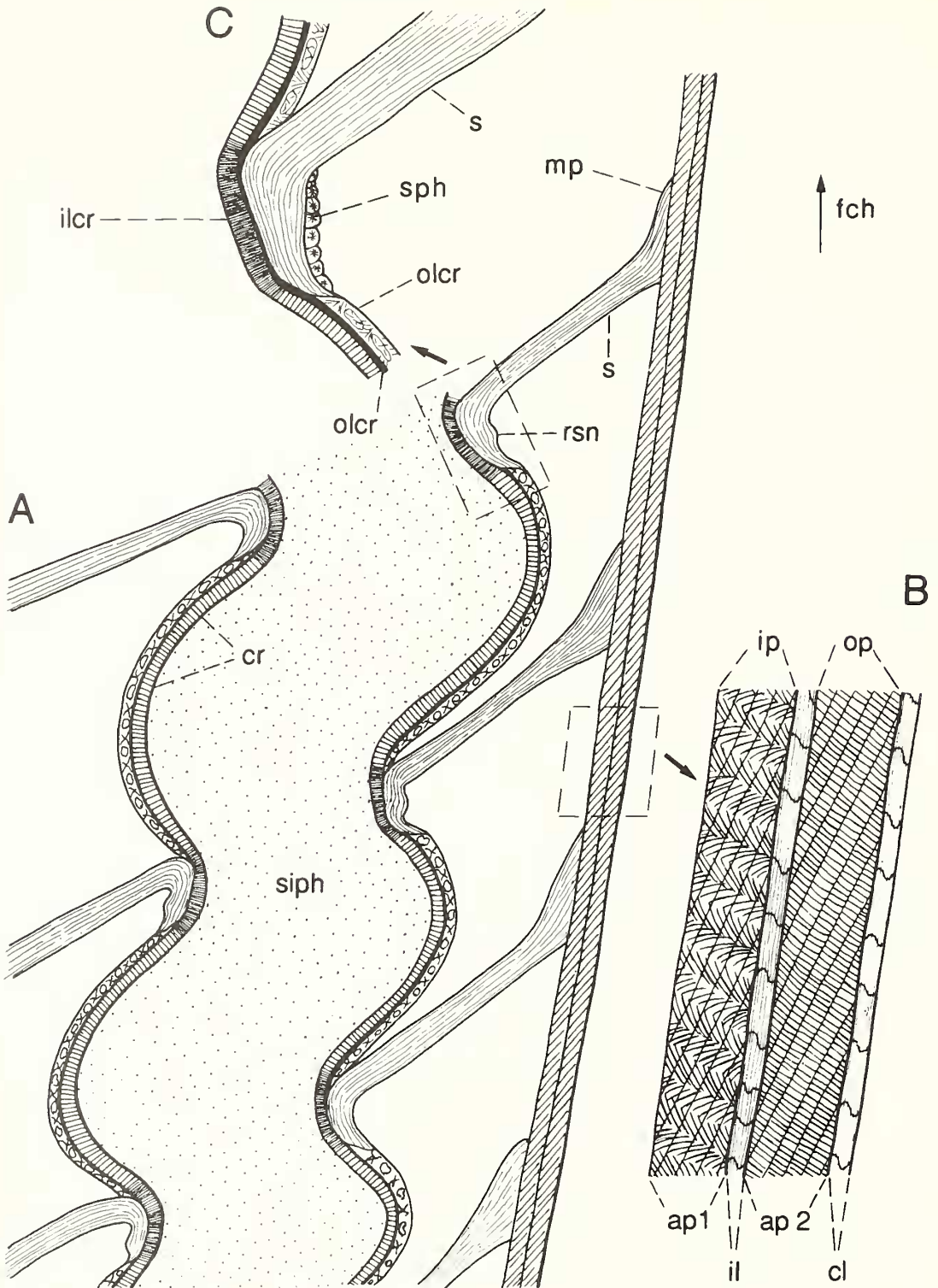
THE Mesozoic record of the spirulids is still inadequately known and until now only two rare taxa were recorded: the Santonian–Maastrichtian *Naefia neogaeia*, and the Maastrichtian *Groenlandibelus rosenkrantzi*. The coleoids are markedly similar in phragmocone structure, but different in their pro-ostracum. Comparison at early ontogenetic stages is still lacking as the initial portions of the shell have not yet been described in the former genus.

Naefia, assigned to *N. kabanovi* sp. nov., together with a previously unknown phragmocone-bearing coleoid, here described as *Adygeya adygensis* gen. et sp. nov., were found in Aptian concretions in north-western Caucasus, Russia (in the valley of the Hokodz River in the Belaya River Basin; see Doguzhaeva 1995). Well-preserved shell material of both taxa allowed examination of their shell ultrastructure and comparison of it with that of Recent *Spirula*. The ultrastructural studies of *Naefia* revealed a great similarity of its siphuncle to that in *Groenlandibelus* and gave additional evidence for placement of this genus within the order Spirulida. SEM studies of *Adygeya* showed that its shell wall, being composed of outer and inner plates, is similar to that of Recent *Spirula*, so this genus was assigned to Spirulida also.

PREVIOUS STUDIES

Naefia was previously known from the Campanian–Maastrichtian of Chile (Wetzel 1930; Biro-Bagoczky 1982; Stinnesbeck 1986), Antarctica (Wetzel 1930; Stilwell and Zinsmeister 1987), south India (Doyle 1986) and from the Santonian–Campanian boundary beds of Japan (Hewitt *et al.* 1991). *Groenlandibelus* is known from Upper Maastrichtian of West Greenland (Jeletzky 1966).

Jeletzky (1966) united *Groenlandibelus* and *Naefia* in the family Groenlandibelidae, on the



TEXT-FIG. 1. For caption see opposite.

assumption that *Naefia*, like *Groenlandibelus*, possessed a caecum and a prosiphon. He included (1966, p. 107) this family, together with Spirulidae, in the order Sepiida on the basis of a supposed common ancestry. According to Jeletzky, groenlandibelids represented early specialized sepiids with a longiconic phragmocone and weakly developed (or absent?) rostrum. Donovan (1977, p. 24), however, excluded *Groenlandibelus* and *Spirula* from Sepiida on the basis of the overall morphology of the phragmocone.

Birkelund and Hansen (1974) studied the ultrastructure of the phragmocone, rostrum and septa in *Groenlandibelus* and came to the conclusion that *Groenlandibelus* was an aberrant genus of uncertain taxonomic position. Nevertheless, these authors emphasized that the possession of a caecum and a prosiphon were strong evidence for referring *Groenlandibelus* to Sepiida *sensu* Jeletzky. Later, Reitner and Engeser (1982) followed Donovan (1977) and reintroduced the order Spirulida, in which they included groenlandibelids. *Naefia* was placed by Engeser (1990) in Coleoidea *incertae sedis*, because of the shortage of morphological data in this genus. Doyle *et al.* (1994) placed the family Groenlandibelidae within the order Spirulida which is included by these authors in the superorder Decabranchia.

MATERIAL AND METHODS

The fossil coleoid shells were collected by the author from Aptian sideritic concretions in the valley of the Hokodz River, some 2–5 km below the village of Hokodz, in the Belaya River basin, in the north-western Caucasus (Russia).

The available material comprises: (1) a single phragmocone fragment of *Adygeya* gen. nov. Its maximum diameter is 22 mm and length 20 mm. It includes seven partly preserved septa. It is only slightly altered diagenetically, so the structure of the shell wall, septal necks and connecting rings could be studied in detail. (2) Six fragments of slender orthoconic phragmocones of *Naefia*. The largest phragmocone is 4.5 mm in diameter, and 13 mm in length. It has nine preserved septa, preceding the extremely short final chamber. The smallest phragmocone is 3 mm in diameter, and 9 mm in length. It has seven preserved camerae. The good preservation of this material allowed detailed study of the shell wall, siphuncle and shell/body attachment scars. Some 30 shells of *Spirula* were collected by Dr Moscalev (Institute of Oceanography of the Russian Academy of Sciences) from Cuba.

The following material was studied with SEM: (1) three oblique sections and one median section of the shell in *Adygeya* gen. nov.; (2) medial sections of two phragmocones and the surface of internal moulds of two phragmocones showing dorsal unpaired shell/body attachment scars in *Naefia*; and (3) ten median sections, six cross sections, and five fragments of the fractured shells with exposed inner surface of the camerae at different ontogenetic stages in Recent *Spirula*. To prevent crushing, the latter were embedded in plastic before cutting. Sections were polished with graded diamond pastes, etched for 3–6 seconds with 1 per cent. HCl and coated with gold. The specimens were examined with a Stereo-Scan S4/10 at the Palaeontological Institute of the Russian Academy of Sciences, Moscow and with a Philips SEM 515 at the Swedish Museum of Natural History, Stockholm.

All material listed above is deposited in collection No. 3871 of the Palaeontological Institute of the Russian Academy of Sciences.

TEXT-FIG. 1A–C. *Adygeya adygensis* gen. et sp. nov.; siphuncular tube (A, C) and shell wall (A–B) in median section; A, $\times 20$; B, $\times 100$; C, $\times 35$. Legend to Text-figures 1–3: a, aperture; apl, acicular-prismatic layer of the inner plate; ap2, acicular-prismatic layer of the outer plate; as, attachment scar; aux, auxiliary deposits; cl, coating layer; cr, connecting ring; f, flap; gl, growth lines; il, intermediate layer; ilcr, inner layer of connecting ring; ip, inner plate of shell wall; mp, mural part of septum; mr, mural ridge; nac, nacreous layer; olcr, outer layer of connecting ring; op, outer plate of a shell wall; r, rim; rsn, retrochoanitic septal neck; s, septum; shw, shell wall; siph, siphuncle; sph, spherulitic-prismatic covering of outer surface of septal neck.

GEOLOGICAL SETTING

The studied coleoids were found in concretions together with Aptian ammonoids belonging to the following genera: *Ptychoceras*, *Acanthohoplites*, *Diadochoceras*, *Nodosohoplites*, *Hypacanthoplites* and *Melchiorites*. The concretions also contained ammonoids with a longer stratigraphical range: *Euphyloceras*, *Phyllopachyceras*, *Tetragonites* and *Gabbioceras*. The rest of the cephalopod fauna comprises the belemnite *Mesohibolites*, and the orthocerid *Zhuravlevia* Doguzhaeva, 1995.

The local Aptian strata include sandstones, siltstones and clays with sideritic concretions, c. 0.2–0.5 m in diameter, some containing as many as 20 ammonoid shells. In the sediments, the abundance of quartz gravel, and numerous pieces of carbonized wood, some large, indicates that these sediments were deposited in a nearshore environment (see Doguzhaeva 1995). The Aptian section is well dated by ammonoids, and five ammonoid zones have been proved in the region (Egoyan 1969). The coleoids under consideration occur in the uppermost zone of *Diadochoceras nodosocostatum* and *Acanthohoplites bigoureti*.

TERMINOLOGY

The following terms are used to describe the shell wall structure in *Adygeya*, *Naefia* and *Spirula*.

Coating layer (Text-figs 1B; 2A). This is the outermost lamellar layer of the shell wall consisting of alternate organic and calcified lamellae; it is considered to be secreted from the outside of the final, or body, chamber. It corresponds to the outer portion of the outer plate as described by Appellöf (1893). The term was introduced first to define the lamellar layer covering the shell of the Late Cretaceous ammonite *Gaudryceras* (Druschitc *et al.* 1978). On the basis of the relationship between the coating layer and the shell proper in *Gaudryceras* it was concluded that the shell became internal at an early ontogenetic stage. Thus, the coating layer had a similar origin to that of the rostrum, in being secreted outside the final, or body, chamber. This conclusion was confirmed by Birkelund (1981) and received further attention in shell wall studies of the Early Cretaceous *Ptychoceras* and *Aconeceras* (Doguzhaeva and Mutvei 1989, 1991).

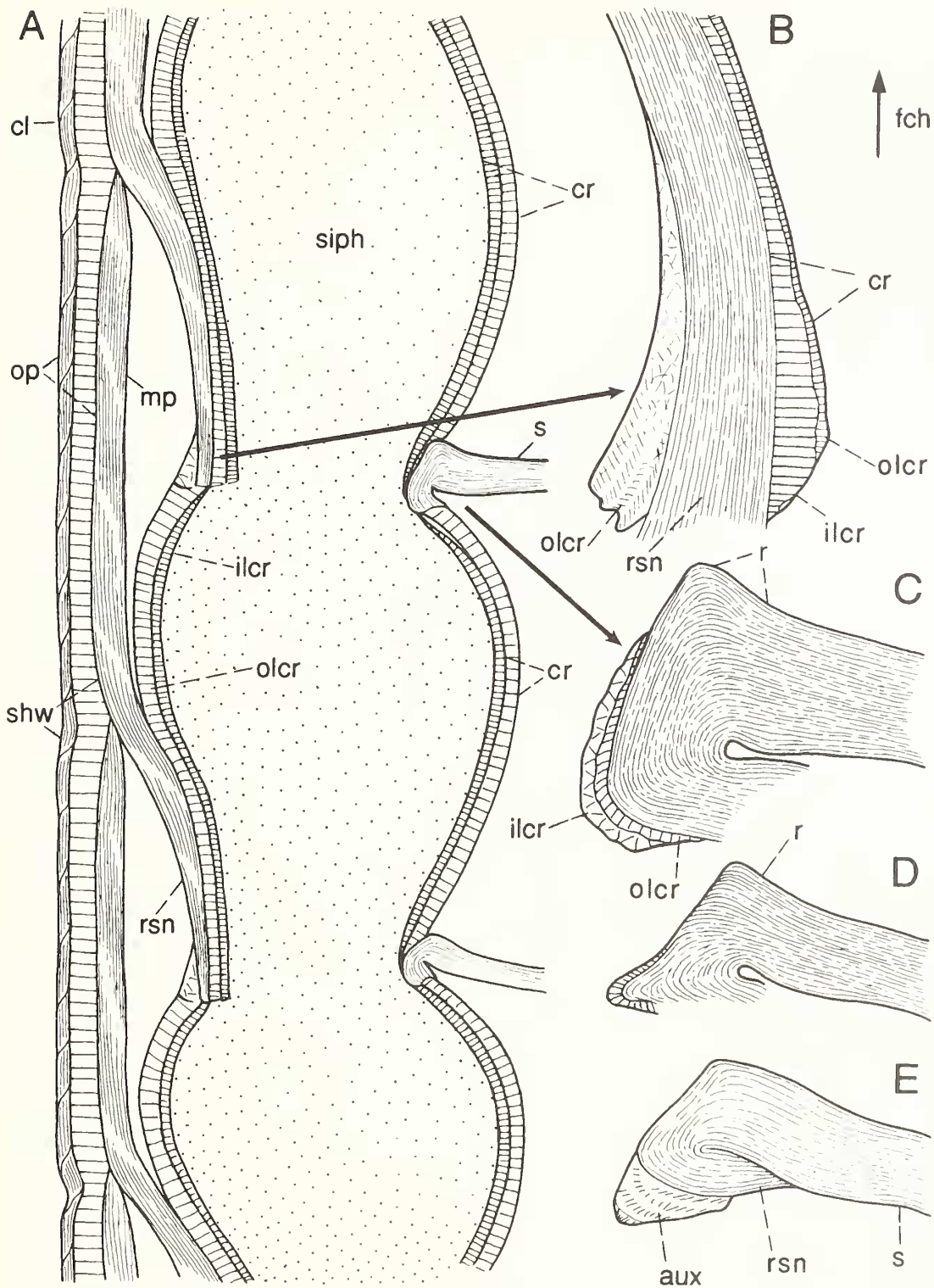
Final chamber. The final portion of the shell between the last septum and the aperture, in ectocochleates it corresponds to the body chamber; in coleoids it houses the rear portion of the body which secretes the septa and the inner part of the shell wall. The term is introduced to emphasize the absence of a chamber which could house the whole body in endocochleate cephalopods.

Guardlike sheath. This is the sheath-like structure of sepiids. According to Jeletzky, who introduced the term, the rostra, tela and guard-like sheaths arose independently in the Belemnitida, Aulacocerida and Tertiary Sepiida. They represent 'convergent evolutionary development resulting in far-reaching homeomorphical similarities of the animals concerned' (Jeletzky 1966, p. 10). The term corresponds to the outer plate of Appellöf (1893).

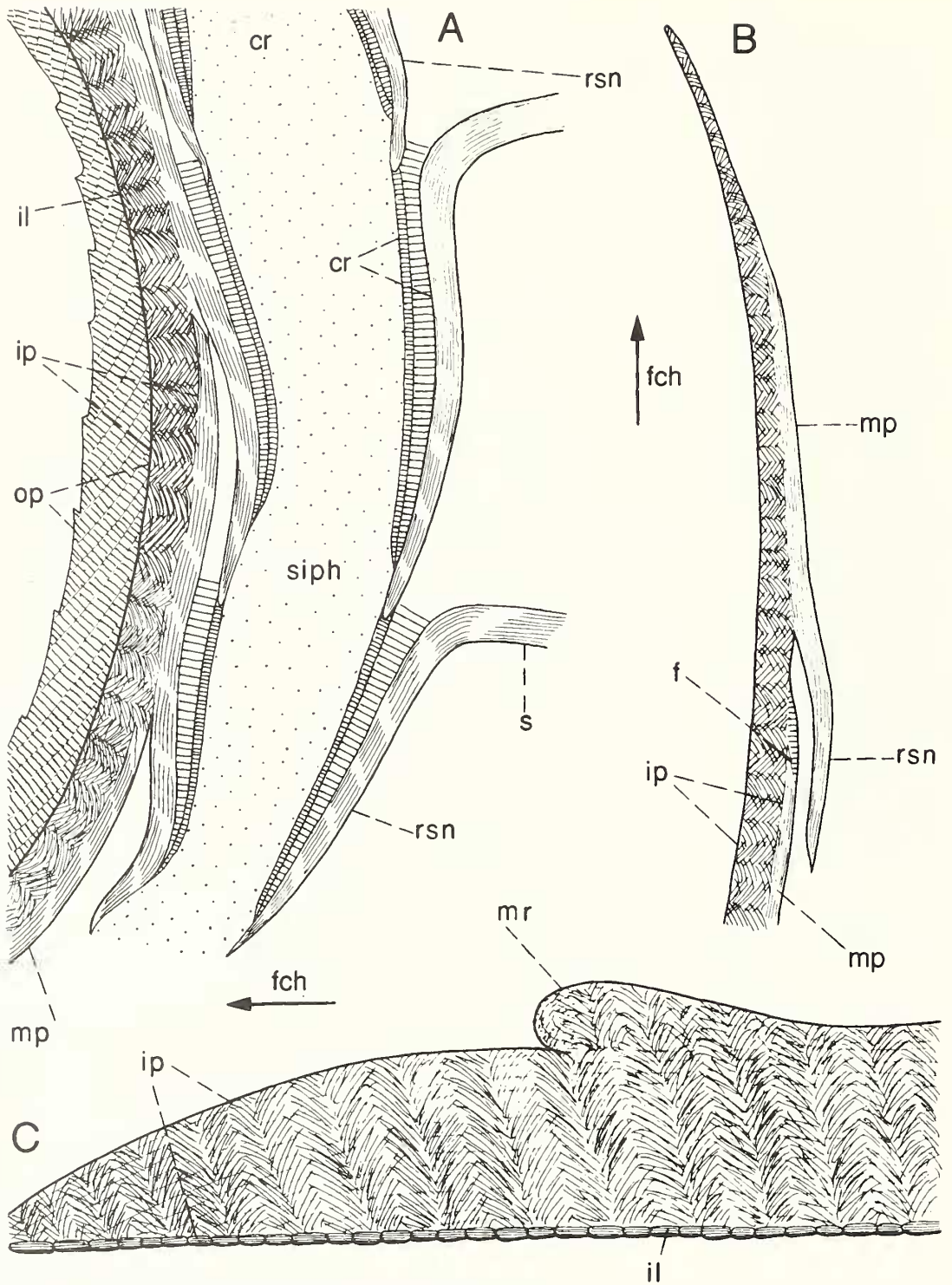
Inner acicular-prismatic layer (Text-figs 1A–C; 3A–B). This is the inner, principal layer of the shell wall characterized by the strongly oblique growth lines and a dendritic pattern formed by acicular crystallites arranged into inclined prisms; it corresponds to the inner plate of Appellöf (1893).

Inner and outer plates (Text-figs 1A–B; 2A, 3A–C). These are the inner and outer portions of the shell wall separated by a distinct interruption. The term was introduced by Appellöf (1893) and applied

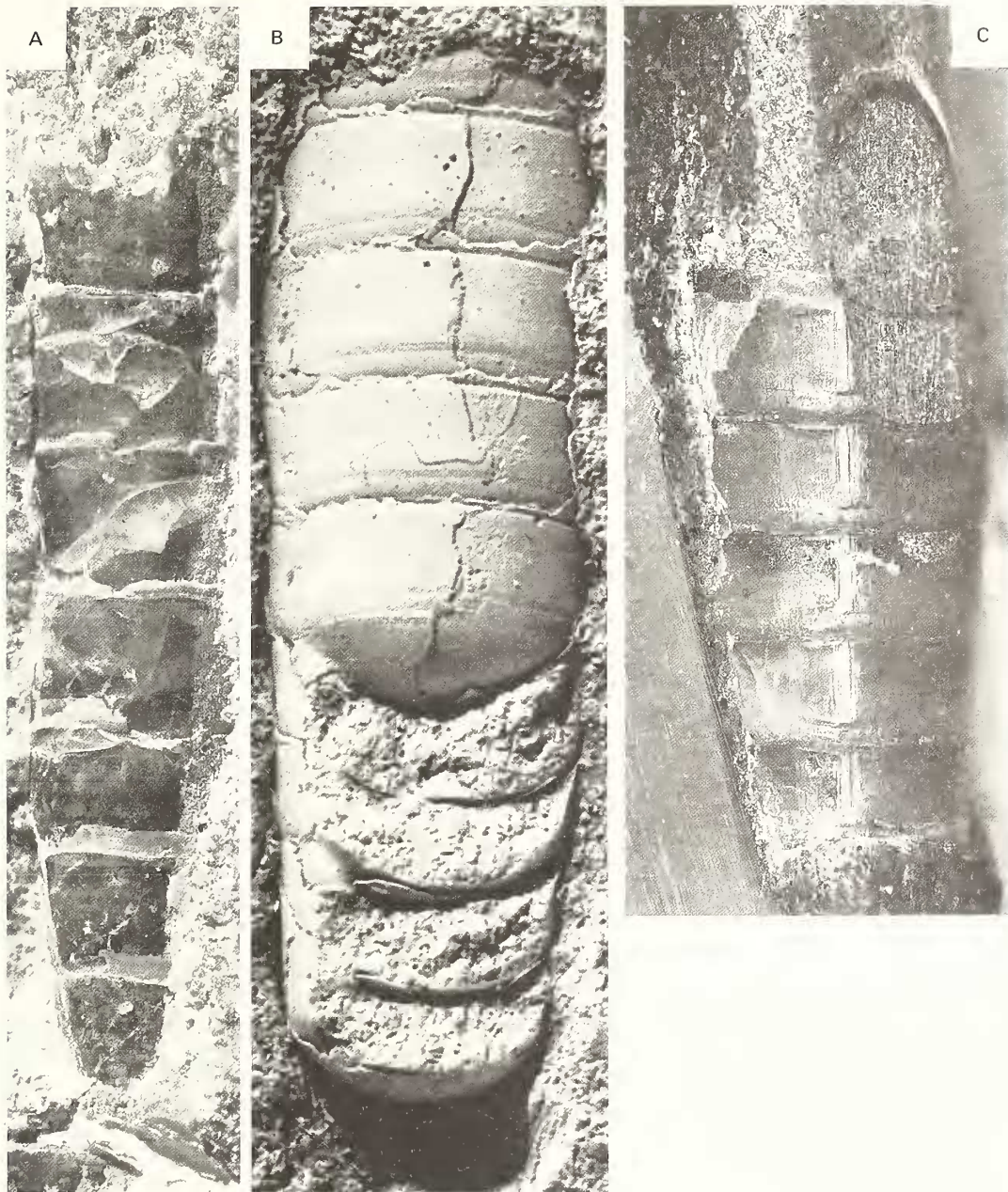
TEXT-FIG. 2A–E. *Naefia kabanovi* sp. nov. A, siphuncular tube and shell wall; $\times 70$. B–C, enlarged detail of A: last septal neck from the ventral (B) and dorsal (C) sides; $\times 300$. D, dorsal portion of a septal neck with adorally directed rim; $\times 300$. E, cyrtocoanitic dorsal septal neck; $\times 350$. For legend see caption for Text-figure 1.



TEXT-FIG. 2. For caption see opposite.



TEXT-FIG. 3A-C. *Spirula spirula*. A, siphuncular tube; $\times 70$. B-C, shell wall; B, $\times 60$; C, $\times 180$. For legend see caption for Text-figure 1.



TEXT-FIG. 4A-C. *Naefia kabanovi* sp. nov.; Upper Aptian, River Hokodz, north-western Caucasus. A, 3871/126; lateral view of the phragmocone, with seven preserved camerae; $\times 16$. B, 3871/124, holotype; lateral view of phragmocone, with two visible retrochoanitic septal necks and eight preserved camerae; $\times 14$. C, 3871/125; dorsal view of phragmocone, with shell/body attachment scars (dorsal line); $\times 9$.

to the shell wall of *Spirula*. It emphasizes the distinct separation of the inner and outer portions of the shell. Later, Chun showed that the interruption in the shell wall of *Spirula* is caused by the attachment of the longitudinal muscles near the aperture where the outer plate is still absent; it appears near the fourth camera on the ventral side and at the penultimate camera on the dorsal side (Chun 1898–99, p. 332, fig. 38).

Intermediate layer (Text-figs 1B; 3A–C). This is a predominantly organic, partly calcified layer between the inner and the outer plates of Appellöf, and corresponding to the assumed periostracum in *Spirula* (Mutvei 1964).

Lamello-fibrillar nacre. Each mineral lamella consists of numerous parallel aragonite rods with a different orientation in consecutive lamellae; the intralamellar organic membranes which subdivide the septal nacre into thin mineral lamellae in the ectocochleate cephalopods are absent here; in sections the rods give an impression of a granular structure, in contrast with tabular nacre with its predominantly hexagonal aragonite crystals which in sections look like columns of tabulae. Lamello-fibrillar nacre forms the septa of *Spirula*, *Sepia*, *Naefia*, *Groenlandibelus*, *Adygeya* and belemnites, whereas the tabular nacre composes the septa and the nacreous layer of the shell wall in Recent *Nautilus*, orhoceroids, bactritoids and ammonoids.

Outer acicular-prismatic layer (Text-figs 1A–B; 3A). This is the outer, principal layer of the shell wall, lying outside the intermediate layer. It consists of acicular prisms arranged perpendicular to the growth lines, and it corresponds to the inner portion of the outer plate of Appellöf (1893).

SYSTEMATIC PALAEONTOLOGY

Subclass COLEOIDEA Bather, 1888

Order SPIRULIDA Stolley, 1919

Family ADYGEYIDAE fam. nov.

Type genus. *Adygeya* gen. nov.

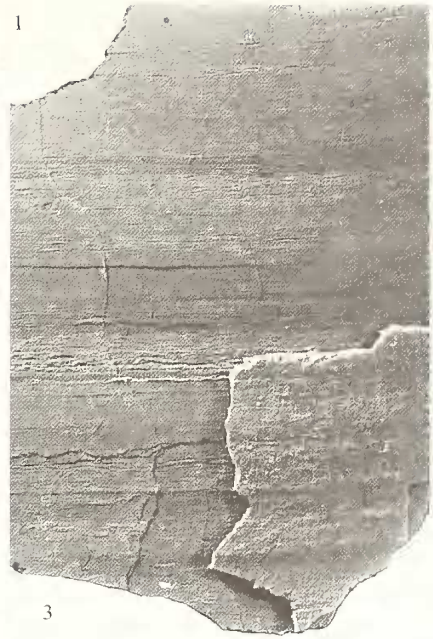
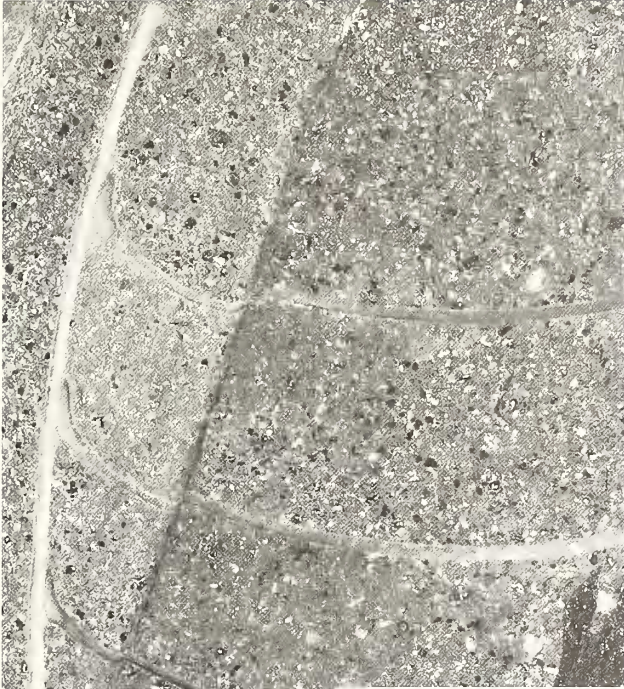
Diagnosis. Shell either orthoconic or slightly exogastrically cyrtconic with comparatively long camerae; rostrum not developed. Surface with thin longitudinal and transverse striations and weak undulations at sutures. Siphuncle comparatively wide, sub-ventral, strongly expanded within camerae. Septal necks short; cyrtchoanitic. Connecting rings thick and calcified. Final chamber short; its length less than the distance between two consecutive septa. Shell wall and septa are of about the same thickness. Shell wall is prismatic, subdivided by the intermediate layer into the inner and outer plates. The inner plate consists of a single acicular-prismatic layer; the outer plate is composed of acicular-prismatic and coating layers.

Range and distribution. Lower Cretaceous, Aptian of the north-western Caucasus.

Remarks. The description is based on the adult shell; early growth stages are unknown. The family is established on the basis of the following features: (1) the orthoconic or slightly cyrtconic

EXPLANATION OF PLATE I

Figs 1–3. *Adygeya adygensis* gen. et sp. nov.; 3871/127; Upper Aptian, River Hokodz, north-western Caucasus. 1, tangential section through phragmocone, showing length of camerae and sub-ventral siphuncle; $\times 8$. 2, detail of fig. 1 showing cyrtchoanitic septal neck; $\times 16$. 3, external view of holotype (ventro-lateral side) with exposed outer surface of inner and outer plates (the fragment of the latter is in the right bottom corner). Uneven longitudinal and transverse striation and weak undulations near septa are visible; the outer plate shows reticulated sculpture; $\times 10$.



1

3

2



phragmocone has a comparatively large diameter; (2) the ventral and dorsal portions of the septal neck are short; (3) the mural parts of the septa are short; (4) the shell wall is prismatic, subdivided by the intermediate layer into the outer and inner plates; and (5) the outer plate consists of the acicular-prismatic and coating layers and the inner plate of the acicular-prismatic layer. In contrast, the family Groenlandibelidae is characterized by: (1) slender phragmocones; (2) long ventral and short dorsal portions of the septal necks; (3) long ventral and short dorsal mural parts of the septa; (4) the absence of a distinct intermediate layer in the shell wall; and (5) the outer plate being represented by a single coating layer, the acicular-prismatic layer being absent. Besides this, the anterior ends of the mural parts of the septa are covered by the innermost portions of the shell wall, in contrast to the condition in the *Adygeyidae*.

The family is referred to *Spirulida* because in *Adygeya* as well as in *Spirula* (1) the well-developed phragmocone possesses comparatively long camerae and a wide marginal siphuncle; (2) the final chamber is short; (3) a rostrum is absent; (4) the shell wall is subdivided by the intermediate predominantly organic layer into the inner and the outer plates; and (5) the inner plate is composed of a single acicular-prismatic layer and the outer plate consists of two layers, the acicular-prismatic and coating layers.

Genus ADYGEYA gen. nov.

Derivation of name. From *Adygeya*, the land of the Circassian native in the north-western Caucasus, where the coleoid was found.

Type species. *Adygeya adygensis* sp. nov.

Type locality. Some 2–5 km below the village Hokodz, in the valley of the Hokodz River, Belaya River Basin, north-western Caucasus.

Horizon. Lower Cretaceous, Upper Aptian (Clansenian).

Diagnosis. The same as for the family.

Adygeya adygensis sp. nov.

Plate 1, figures 1–3; Plate 2, figures 1–4; Plate 3, figures 1–2; Plate 4, figures 1, 4; Plate 5, figures 1–3

Derivation of name. The same as for genus.

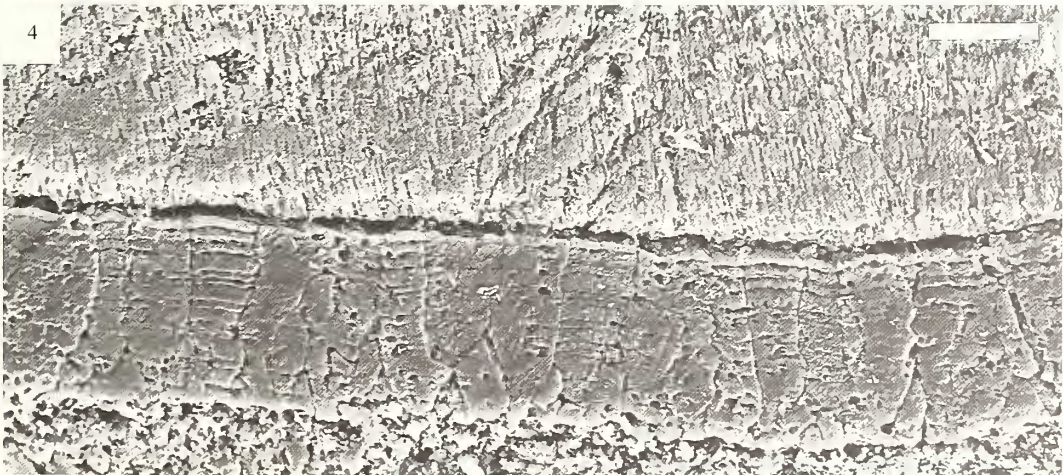
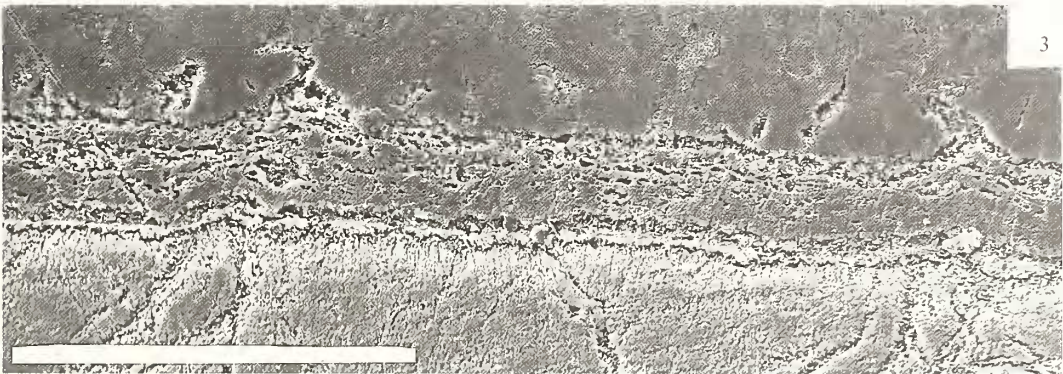
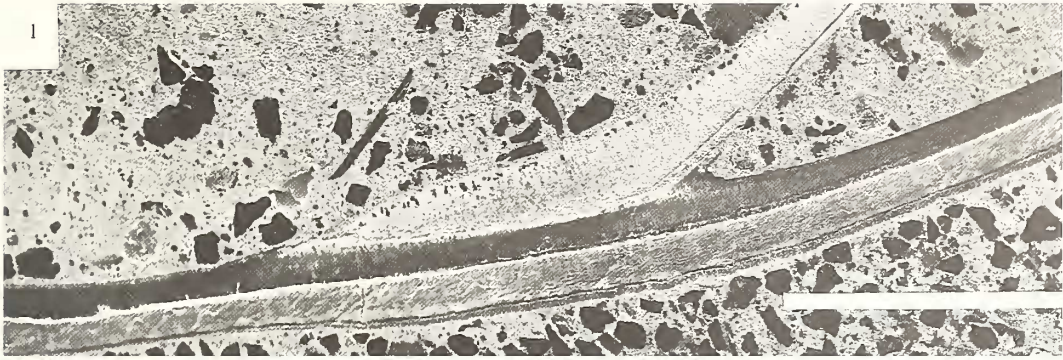
Holotype. 3871/127, in the Palaeontological Institute of the Russian Academy of Sciences.

Type locality. The same as for the genus.

Description. The holotype is a 22 mm long portion of the phragmocone and comprises seven camerae; it is 20 mm in maximum diameter. The shell is an orthocone or a slightly exogastric cyrtocone. In the adult stages there is no evidence for a rostrum. Surface with thin uneven longitudinal and transverse striations and weak undulations near the septa. The comparatively wide siphuncle is sub-ventral, strongly expanding within the camerae. The ratio between the height and width of the siphuncular segments is about 1. Septal foramen oval.

EXPLANATION OF PLATE 2

Figs 1–4. *Adygeya adygensis* gen. et sp. nov.; 3871/127; Upper Aptian, River Hokodz, north-western Caucasus; micrographs of the shell wall in median section. 1, general view of the shell wall, showing inner and outer plates, separated by intermediate layer, and covered by coating layer; scale bar represents 1 mm. 2, detail of fig. 1 showing the indistinct boundary between shell wall and septum, and the continuation of lamellae between them; scale bar represents 0.1 mm. 3, detail of fig. 1, showing porous lamellar structure of the intermediate layer; scale bar represents 0.1 mm. 4, detail of fig. 1, showing coating layer with lamellar structure covering the outer plate; scale bar represents 10 μ m.



Necks are short retrochoanitic. Mural parts of the septa are short. The connecting rings consist of two thick spherulitic-prismatic layers. The adorally preserved camera is about 3.2 mm long along the ventral side; the seventh camera, which is the last preserved, is about 2.2 mm long along the ventral side. Length of the last camera is about 0.1 of its diameter. The final chamber length is estimated as short, less than the length of one camera, on the basis of (1) an absence of the separating boundary between the septa and the shell wall and (2) the strongly oblique growth lines in the inner layers of the shell wall. Both conditions are as observed in *Spirula*. The shell wall consists of the inner and the outer plates, separated by the intermediate layer.

Subclass COLEOIDEA Bather, 1888
Order SPIRULIDA Stolley, 1919
Family GROENLANDIBELIDAE Jeletzky, 1966

Type genus. *Groenlandibelus* Jeletzky, 1966.

Diagnosis. Slender longiconic orthocones with regular contractions near sutures, long camerae and a comparatively wide, ventral siphuncle. Siphuncle begins with a caecum and prosiphon within the protoconch. Ventral mural parts of the septa as long as the distance between the two septa; dorsal parts short. Septal necks retrochoanitic; short cyrtchoanitic dorsally and long holochoanitic ventrally. The last few septal necks on the dorsal side look to be transitional to prochoanitic. Segments swollen. Connecting rings spherulitic-prismatic. Final chamber short, as long as camerae. Rostrum absent or restricted to the earliest portion of the phragmocone. Shell wall consists of prismatic and coating layers.

Range and distribution. Upper Aptian of north-western Caucasus; Santonian–Campanian boundary of Japan; Campanian–Maastrichtian of Chile, south India, Antarctic Peninsula; Upper Maastrichtian of West Greenland.

Genus NAEFIA Wetzel, 1930

Type species. *Naefia neogaeia* Wetzel, 1930.

Type locality. Chile.

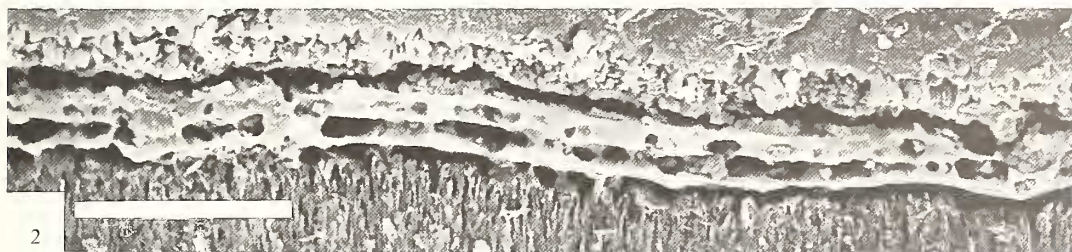
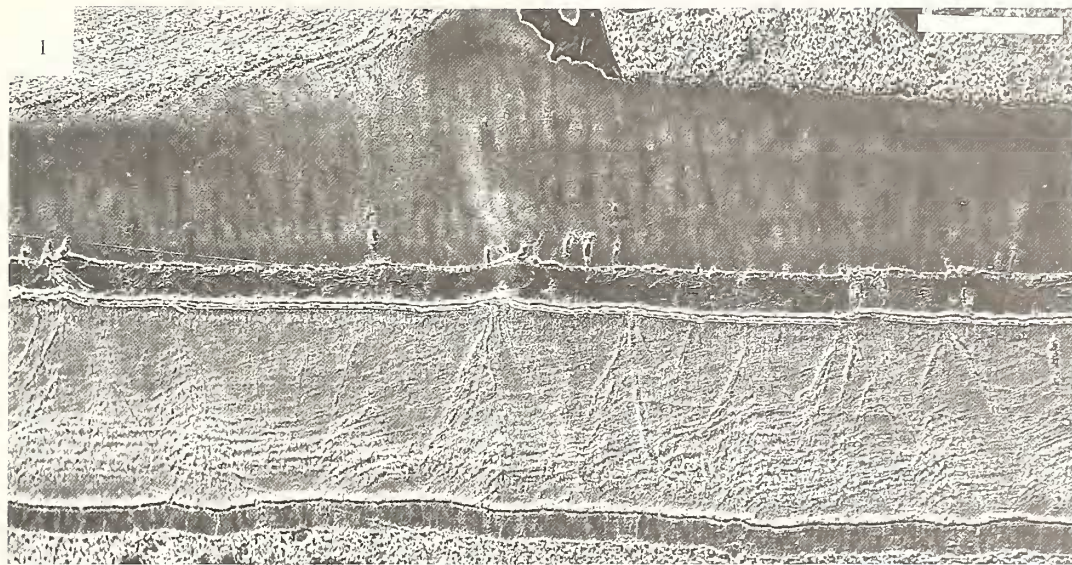
Diagnosis. The same as for the family, with the following additions: dorsal unpaired shell/body attachment scars occur on inner surface of each camera; they are narrow and as long as a camera; pro-ostracum is narrow with broad median field.

Range. Same as for family.

Remarks. Differs from *Groenlandibelus* in the structure of the pro-ostracum: the median field is relatively broad in *Naefia* (Doyle, 1986), but narrow in *Groenlandibelus*. Since early growth stages are not known, the comparison with *Groenlandibelus* cannot be complete. The distinct similarity between *Naefia* and *Groenlandibelus* was pointed out by Birkelund (1956), Jeletzky (1966) and Doyle (1986). The structure of the siphuncle, described here, stresses this resemblance. This justifies the assignment of *Naefia* within the Groenlandibelidae.

EXPLANATION OF PLATE 3

- Figs 1–2. *Adygeya adygensis* gen. et sp. nov.; 3871/127; Upper Aptian, River Hokodz, north-western Caucasus. 1, inner plate (top), intermediate layer, outer plate and coating layer of the shell wall (see also Pl. 2, fig. 1); scale bar represents 0.1 mm. 2, detail of fig. 1 showing the organic lamellae within the intermediate layer. Scale bar represents 10 μ m.
- Fig. 3. *Spirula spirula*; 3871/128; Cuba; shell wall, showing inner and outer plates, separated by intermediate layer; scale bar represents 0.1 mm.



Naefia kabanovi sp. nov.

Plate 6, figures 1–5; Plate 7, figures 1–2; Plate 8, figures 1–4; Plate 9, figures 1–3; Text-figure 4

Derivation of name. In honour of G. K. Kabanov, the expert in Cretaceous belemnites, to whom I am grateful for the joint expeditions to the Volga River region.

Holotype. 3871/124, in the Palaeontological Institute, Russian Academy of Sciences.

Type locality. Some 2–5 km below the village Hokodz, Hokodz River valley, Belaya River Basin, north-western Caucasus.

Description. Slender longiconic orthocones, circular in cross section. Angle of expansion 12–14° at early ontogenetic stages to 7–9° at adult stage. Shell surface with fine, uneven longitudinal and transverse striations, and weak undulations near sutures. Inner ventral shell surface with regular contractions at intervals equal to number of camerae. Camerae long, about 30 per cent. of the shell diameter. Sutures normal, with small ventral and dorsal lobes. Siphuncle wide, expanded within camerae, ventral: submarginal at early ontogenetic stages then marginal. Siphuncular diameter is about 20 per cent. of that of the phragmocone at the septal necks; diameter of the septal foramen is about 65 per cent. of the siphuncular segment. The ratio of segment length to maximum diameter is about 1.3–1.5 to 1.0. Septal necks retrochoanitic, short cyrtochoanitic dorsally and long subholochoanitic ventrally. The last few septal necks on the dorsal side look transitional to prochoanitic due to a thickened, adoral rim. Connecting rings consist of two spherulitic-prismatic layers. Mural parts of septa are short dorsally and as long as the camerae ventrally. Final chamber is short, its length equal to the distance between two consecutive septa. Shell wall prismatic with thin coating layer. It is thicker ventrally than dorsally, the ventral wall together with mural parts of septa being about three times thicker than the dorsal wall. On dorsal side, a thin inner portion of shell wall forms flaps covering mural parts of septa. The flap at the adult aperture is prominent.

Remarks. In *N. kabanovi* the sutures are normal to the shell axis whereas in *N. neogaeia* Wetzel, 1930 they are slightly oblique.

The siphuncular structures in *N. neogaeia*, as well as the shell wall/body attachment scars are not known, so the comparison with the latter is restricted to external morphology and cannot be complete. The pro-ostracum is unknown in *N. kabanovi* but is known in *N. neogaeia*.

SHELL ULTRASTRUCTURE

Previous studies

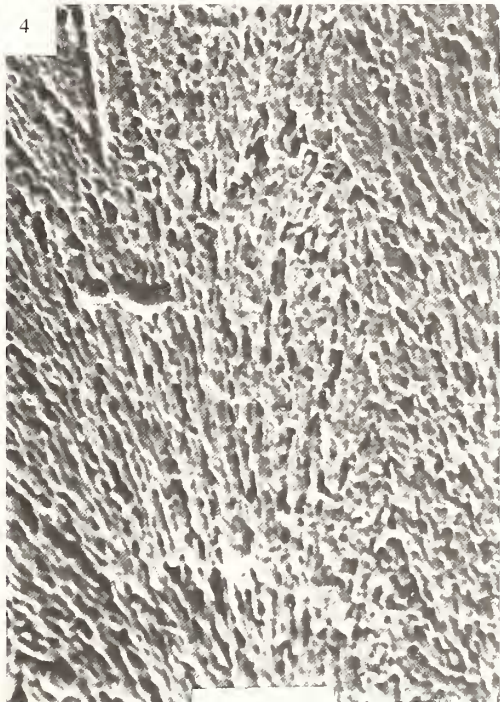
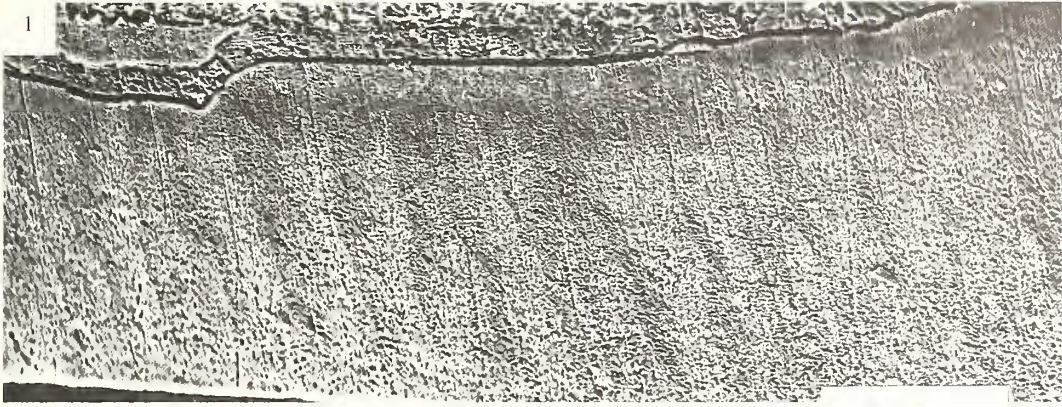
Hewitt *et al.* (1991) found that in *Naefia* the shell wall consists of a thick prismatic layer, invested from outside by a thin lamellar layer which, according to them, could be nacreous. These authors also found that in *Naefia* the septa possess lamello-fibrillar nacre.

Jeletzky (1966) studied the shell structure in the related genus *Groenlandibelus*. According to him, the wall of the phragmocone consists of a prismatic layer, which is more similar in its structure to the internal 'semi-prismatic' layer of the shell in *Spirula* (Mutvei 1964) than to the phragmocone wall in belemnites. In addition, he showed that in *Groenlandibelus* connecting rings are composed

EXPLANATION OF PLATE 4

Figs 1, 4. *Adygeya adygenis* gen. et sp. nov.; 3871/127; Upper Aptian, River Hokodz, north-western Caucasus. 1, inner plate of the shell wall showing oblique vertical bands similar to those in the inner plate of the shell wall in *Spirula* (fig. 2); scale bar represents 0.1 mm. 4, feather-like arrangement of the acicular crystallites within the inner plate, similar to that in *Spirula* (fig. 3); scale bar represents 10 μ m.

Figs 2–3. *Spirula spirula*; 3871/128; Cuba. 2, shell wall, showing inner plate and thin outer plate, separated by intermediate layer; inner plate is similar to that in *A. adygenis* (fig. 1) in showing oblique vertical bands; scale bar represents 0.1 mm. 3, feather-like arrangement of the acicular crystallites within the inner plate, similar to that in *A. adygenis* (fig. 4); scale bar represents 10 μ m.



of two, partly calcified layers; septa are built up of irregularly oriented granulae or spiculae; mural parts possess a considerable amount of organic matter in the calcium carbonate.

Birkelund and Hansen (1974) also studied the shell ultrastructure in *Groenlandibelus*, and compared it with that in the other coleoids. According to them, the nacreous septa are of granular structure, without intralamellar membranes. This feature allies the genus to Belemnitida, while the unilayered, prismatic phragmocone wall allies it to Sepiida.

Shell wall in Adygeya, Naefia and Spirula

Adygeya. The shell wall is preserved on the ventral and ventro-lateral sides. It is characterized by the absence of the nacreous layer (Pl. 3, fig. 1; Text-fig. 1A–B), fine reticular sculpture (Pl. 1, fig. 3) and in being thin (Pl. 1, figs 1–2). By contrast with the ectocochleates, in *Adygeya* the shell wall has approximately the same thickness as the septa. It consists of the inner and the outer plates separated by the intermediate layer (Pl. 2, fig. 1; Text-fig. 1A–B).

1. The inner plate is represented by the inner, principal acicular-prismatic layer. It is about one-third to one-half of the total thickness of the shell wall (Pl. 2, fig. 1). The layer is composed of prisms, about 0.01–0.02 mm wide, with a dendritic structure, formed by a feather-like arrangement of acicular crystallites in each prism (Pl. 4, fig. 4). The growth lines are oblique and oriented approximately at the same angle as those in the outer principal layer. Median sections of this layer show alternation of dark and light, branched vertical bands which are slightly inclined forward (Pl. 3, fig. 1). The orientation of the bands follows the orientation of the long axes along which the crystallites are grouped, forming a dendritic pattern. The bands are assumed to be organic matter between vertical prisms. In addition, in etched preparations, narrow interspaces, probably filled originally by organic matrix, are observed between the crystallites and bundles of crystallites. A narrow outermost zone of the layer has a compact structure.

2. The intermediate layer is thin, about one-eighth the shell wall thickness. It is made up of alternate organic and calcified lamellae (Pl. 2, fig. 3). The layer is preserved only partially; in most places it can be recognized as a crack. The outer plate is represented by the acicular-prismatic layer and the coating layer.

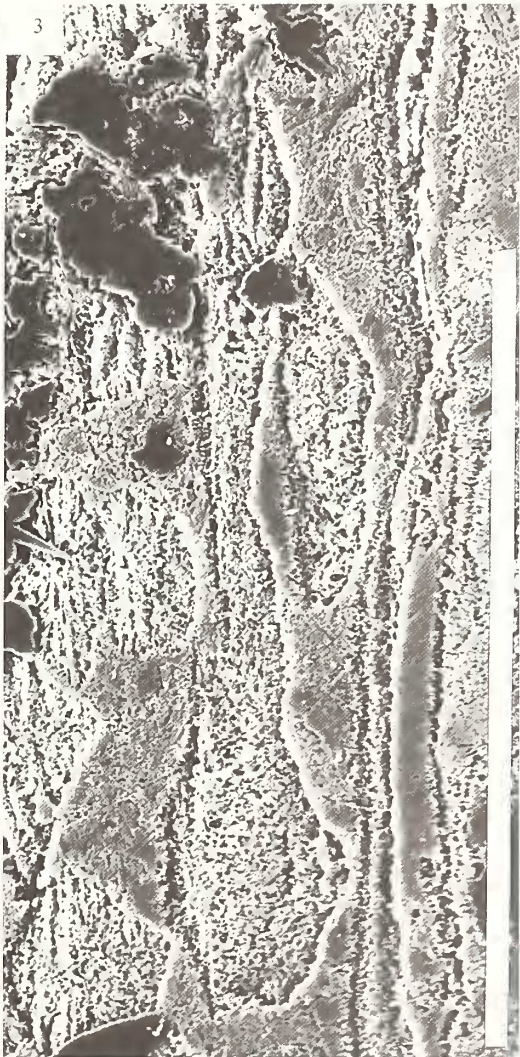
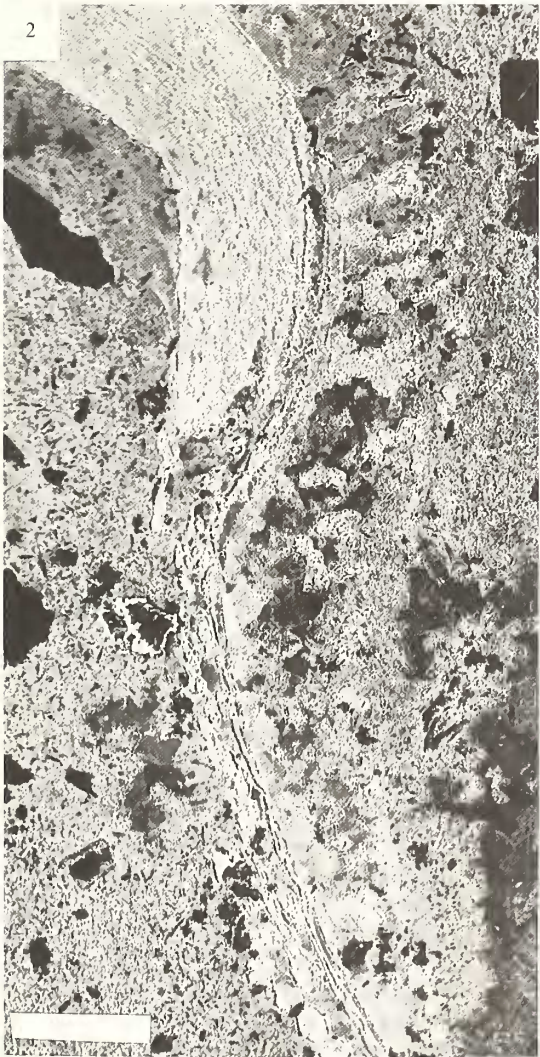
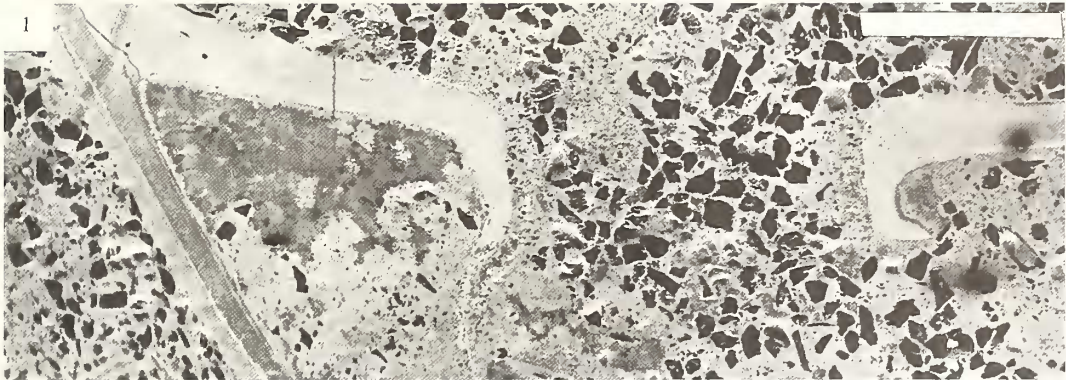
3. The outer principal acicular-prismatic layer comprises about one-third the total thickness of the shell wall (Pl. 2, fig. 1). It shows numerous, closely spaced, distinct, oblique growth lines which have a slightly wavy course and which run at the angle of about 25° towards the aperture (Pl. 3, fig. 1). The layer has a simple prismatic structure consisting of acicular crystallites which are oriented more or less vertically (Pl. 2, fig. 4; Pl. 3, fig. 3).

4. The coating layer is a thin lamellar layer which has a thickness equal to about one-eighth the wall thickness (Pl. 2, figs 1, 4). It seems to consist of alternate uneven organic and calcified lamellae lying parallel to the surface of the wall. Calcified lamellae seem to be composed of irregularly sized prisms, about 5 μm wide, made up of acicular crystallites. The thickness of the lamellae varies between 1 and 2 μm.

Between the inner surface of the shell wall and the septa there is no distinct boundary. At the ultrastructural level, this indistinct boundary is caused by the fact that the lamellae in the septa and in the dendritic prisms of the shell wall are continuous, despite the ultrastructural differences (Pl. 2, fig. 2). An extremely thin, probably organic film lines the adoral septal surface and the shell wall (Pl. 2, fig. 1).

EXPLANATION OF PLATE 5

Figs 1–3. *Adygeya adygensis* gen. et sp. nov.; 3871/127; Upper Aptian; River Hokodz; north-western Caucasus. 1, septal necks with a partly preserved connecting ring; scale bar represents 1 mm. 2, enlarged detail of fig. 1 to show that the connecting ring is composed of two porous, comparatively thick, spherulitic-prismatic layers separated by a thin organic layer; scale bar represents 0.1 mm. 3, enlarged detail of fig. 2 to show the flattened spherulites of the outer layer; scale bar represents 0.1 mm.



DOGUZHAEVA, *Adygeya*

Naefia. The shell wall is characterized by the absence of the nacreous layer (Text-fig. 2A). It is composed of a simple prismatic layer; there are some indications of a thin coating layer (Pl. 6, fig. 3). The shell wall is thin, about the thickness of a septum (Pl. 6, fig. 1). On the ventral side, the inner surface of the shell wall is invested by the long thick mural parts of the septa (Pl. 6, fig. 2). Together they are about three times as thick as the dorsal wall. On the dorsal side, the innermost thin portion of the shell wall covers the anterior ends of the septal mural parts of the septa (Pl. 8, fig. 3). The covering of the mural parts of the last septum is the most prominent (Pl. 9, fig. 1). The boundary between the shell wall and the septa is distinct (Pl. 9, figs 2–3) in contrast to that in *Adygeya*.

The shell/body attachments are visible on the exposed surface of the internal mould of the two phragmocones (Pl. 8, fig. 1; Text-fig. 4C). In each chamber there is a dorsal, unpaired, longitudinal, slender, spindle-shaped scar with width at its maximum near the middle part of a camera, and narrowing towards the posterior and anterior ends (Pl. 8, figs 1–2). The boundary of the scar is distinct along the sides but indistinct near the anterior and posterior ends.

As shown by the SEM micrographs the dorsal scars bear numerous minute pore openings, less than 0.01 mm in diameter (Pl. 8, figs 1–2). Each scar seems to correspond to a dorsal furrow or 'Normallinie' of orthoceroids, bactritoids, belemnoids and aulacocerids, although pores in these furrows are unknown. The pores were previously known in the inner prismatic layer (myostracum) of the Triassic ceratid *Phyllocladiscites*, in the mantle attachment layer at the shell aperture of Recent *Nautilus* (Doguzhaeva and Mutvei 1986a), and in the shell wall of two Lower Cretaceous ammonoids: *Ptychoceras* and *Aconeceras* (Doguzhaeva and Mutvei 1989, 1991). Recently, pores were found on the dorsal furrow of *Mesohibolites* (unpublished data). The occurrence and function of the shell pores in molluscs are still inadequately known; some may strengthen the attachment of the mantle to the shell, notably the pores at the apertural margin of *Nautilus*. In *Naefia* the adhesion between the body and the shell on the dorsal side may have been strengthened by means of the tiny mantle extensions housed inside the pore canals of the dorsal scars.

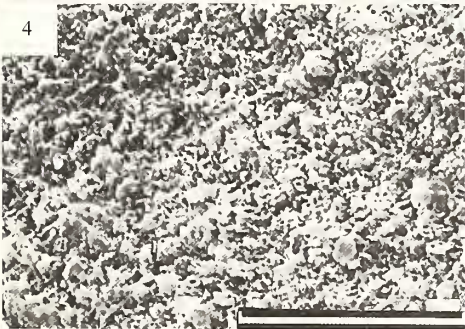
Comparison of the shell wall structure in Adygeya and Spirula

The shell wall in both *Adygeya* and *Spirula* is as thin as the septa and is characterized by the absence of a nacreous layer (Text-figs 1A–B, 3A–C). In both genera it consists of the inner and outer plates separated by the intermediate layer. The inner plate is represented by the inner acicular-prismatic layer with its dendritic structure, which makes up the main part of the shell wall. The intermediate layer is predominantly organic, partly calcified. The outer plate is represented by the outer acicular-prismatic layer, with its simple prismatic structure, and the coating layer with its high content of organic matrix.

The intermediate layer is considered to mark a strong interruption between the secretional zones of the inner and the outer plates. The inner plate seems to have been secreted within the final chamber, whereas the outer plate, on the outer side of the intermediate layer, was formed from the outside of the final chamber. The interruption was probably caused by 'a thick, sharply defined layer of connective tissue (bg.) which extends into the ventral wall of the anterior part of the shell sac', as observed in *Spirula* by Chun (1898–99, p. 335).

EXPLANATION OF PLATE 6

Figs 1–5. *Naefia kabanovi* sp. nov.; 3871/124, holotype; Upper Aptian, River Hokodz, north-western Caucasus. 1, median section of shell, consisting of eight camerae and a short final chamber with preserved apertural margin of shell aperture; scale bar represents 1 mm. 2, detail of fig. 1 showing long mural part of septum and holochoanitic ventral portion of septal neck; scale bar represents 300 μm . 3, prismatic layer of the shell wall on the ventral side and remnants of a thin lamellar coating layer (left side); scale bar represents 30 μm . 4, granular appearance of the nacre Type II in septum; scale bar represents 10 μm . 5, cyrtchoanitic dorsal portion of septal neck with an auxiliary deposit; scale bar represents 30 μm .



The inner plates in both genera under consideration are very similar, perhaps identical; the outer plates differ in the following features: (1) the acicular-prismatic layer is thick, with oblique growth lines in *Adygeya*, but thin with growth lines parallel to the shell wall surface in *Spirula*; (2) the coating layers are structurally different; the lamellar structure is more prominent in *Adygeya* than in *Spirula*. In addition, the shell surface has a fine reticulate pattern in *Adygeya* but a distinct and coarse reticulate ridge-like pattern in *Spirula*.

The intermediate layer in both genera is predominantly organic; in *Spirula* it shows regular vertical membranes which have not been observed in *Adygeya*.

Comparison of the shell wall structure in Naefia and Spirula, with comments on some other coleoids

The shell wall structures in *Naefia* (Text-fig. 2A) and *Spirula* (Text-fig. 3A–C) are similar in: (1) the absence of the nacreous layer; (2) the predominantly prismatic structure of the shell wall; (3) the comparable thickness of the shell wall to that of the septa; (4) the mode of strengthening of the contact between the shell wall and septa by means of secretion of the flaps, septal ridges and lengthening of the ventral mural parts of the septa; and (5) the presence of the coating layer, which, however, in *Naefia* is lamellar and in *Spirula* acicular-prismatic. Thus, in comparison with that in both *Spirula* and *Adygeya*, the shell wall in *Naefia* was modified by elimination of one of the acicular-prismatic layers.

Among the other coleoids, the Late Campanian–Maastrichtian *Actinosepia* (Waage 1965), Cenozoic *Belosepia*, *Vasseuria*, *Beloptera*, *Belopterina* (Dauphin 1984a, 1984b, 1985a, 1985b, 1986) and Recent *Sepia* (Appellöf 1893; Barskov 1973; Bandel and von Boletzky 1979; Dauphin 1981; Bandel 1989) show some similarity in shell wall (dorsal shield) structure to that in *Adygeya* and *Spirula*. In the genera listed above, the dorsal shield is formed of two calcareous portions separated by an intermediate layer, which is highly variable with regard to its degree of mineralization, but is predominantly organic.

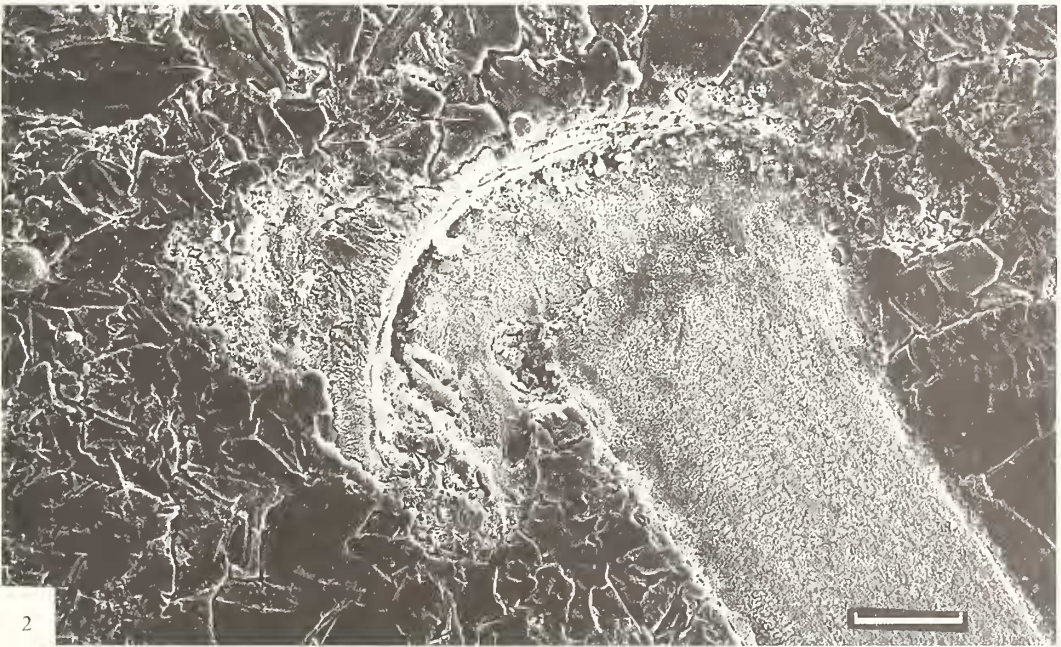
The septa and septal neck structure

Adygeya. Septa are composed of lamello-fibrillar nacre which also forms the septa of *Naefia* and Recent *Spirula*. The adoral septal surface is lined by a thin organic or slightly calcified layer. The mural parts of the septa possess a spherulitic-prismatic structure and, as indicated by their brown colour, seem to contain much organic matrix. Around the siphuncular openings the septa are thicker. The mural parts are thicker than the septa proper. Within the septal necks the organic lamellae are more distinct. The septal structure in *Adygeya* shows great similarity to that in *Groenlandibelus* (Jeletzky 1966; Birkelund and Hansen 1974).

Naefia. The septa and septal necks are formed by lamello-fibrillar nacre. The septal periphery (near the shell wall) possess a nacreous structure with well formed nacreous tablets, but the central part of the septa, as shown by Hewitt *et al.* (1991), has a granular exterior (Pl. 6, figs 4–5; Pl. 7, fig. 2). The adoral surface is covered by an organic sheet (Pl. 9, figs 2–3). Septal necks show distinct organic lamellae, and their distal ends seem to be less calcified (Pl. 7, fig. 1; Pl. 8, fig. 4). The dorsal portions of the last few septal necks show rim-like thickenings directed adorally (Pl. 8, fig. 4; Text-fig. 2C–D),

EXPLANATION OF PLATE 7

Figs 1–2. *Naefia kabanovi* sp. nov.; 3871/124; Upper Aptian, River Hokodz, north-western Caucasus. 1, ventral portion of septal neck lined by thick outer spherulitic-prismatic and thin inner prismatic layer of the connecting ring; the outer surface of the septal neck (left side) is covered by the auxiliary deposit. 2, dorsal portion of the septal neck. Scale bars represent 30 μm .



DOGUZHAeva, *Naefia*

similar to the transitional stage to the prochoanitic septal necks in ammonoids (Doguzhaeva and Mutvei 1986b). Similar, rim-like anterior portions of the septal necks were observed in some Early Cretaceous belemnites (Kabanov 1967; unpublished data).

Connecting ring structure

Adygeya. The connecting rings consist of two porous spherulitic-prismatic layers separated by a thin, probably organic layer (Pl. 5, figs 1–3; Text-fig. 1A, C). The outer layer is a structurally modified continuation of the septal neck; it is composed of flattened spherulites with numerous interspaces (Pl. 5, figs 2–3). The inner layer is composed mainly of elongated prisms or bundles of prisms oriented with their long axes perpendicular to the septal neck and separated by numerous interspaces. At the septal necks the inner layer has about the same thickness as the necks but it grows thinner towards the central part of the camera. The intermediate organic layer lines the septal neck (Pl. 5, fig. 2).

Naefia. The connecting rings consist of two layers (Text-fig. 2A–B). The outer layer is thick spherulitic-prismatic in structure. It seems to represent a structurally modified continuation of a septal neck. The inner layer is thin, probably slightly calcified or organic. The auxiliary deposits are well-developed and give a swollen shape to the ends of the septal necks (Pl. 6, fig. 2; Pl. 7, figs 1–2). The siphuncular structure in *Naefia* is similar in all known details to that in *Groenlandibelus* (Jeletzky 1966).

EVOLUTIONARY IMPLICATIONS

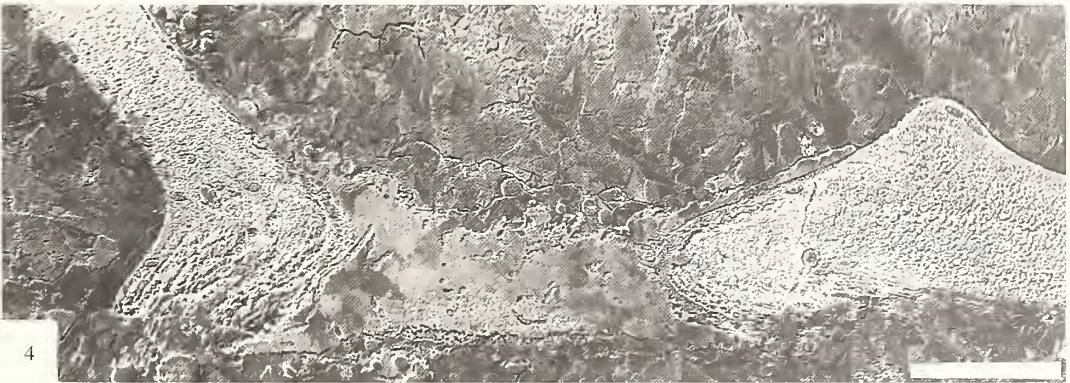
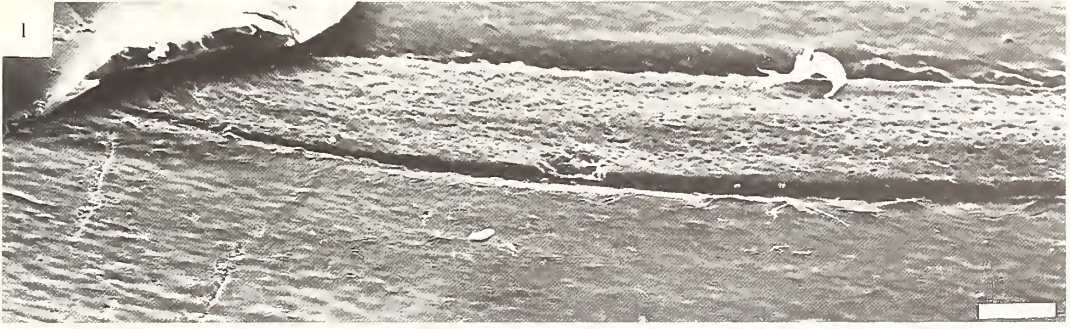
The new Aptian species *N. kabanovi* possesses all the general features which occur in the Late Cretaceous *N. neogaeia*; the structure of the initial portion of the shell is still unknown in both species. There is high stability in the shell morphology of this genus. Moreover, the siphuncular structures, which were previously unknown in *Naefia*, stress the similarity between *Naefia* and *Groenlandibelus* and confirm the placement of *Naefia* within the Groenlandibelidae, which was questioned by Engeser (1990), and the placement of Groenlandibelidae within the order Spirulida (former Sepiida), which was doubted by Meyer (1993).

The family Adygeyidae, comprising the single Aptian genus *Adygeya*, represents another branch, distinctly different from the Groenlandibelidae. This demonstrates the diversity of Early Cretaceous spirulids. The comparison of the shell wall structure in *Adygeya* and *Spirula* leads to the conclusion that in the lineage of Spirulida the shell possessed an outer plate instead of a rostrum. Therefore, the taxa which had a rostrum can hardly be interpreted as precursors of *Spirula*.

This conclusion contradicts the widespread opinion, introduced by Voltz (1830) and elaborated upon by many, but most significantly by Naef (1921–22), of sepiids (including spirulids) being derived from a belemnoid stock by the reduction and loss of a rostrum (Teichert 1988). It follows from this that forms intermediate between belemnoids and sepiids would be expected to possess remnants of the phragmocones and rostra. Jeletzky did not accept Naef's phylogeny. According to him, 'absence of the primordial guard in Sepiida, combined with retarded appearance of the sepiid sheath, and its asymmetrical mode of the growth do not support the interpretation of the sheath as a gradually dorsalward migrating homologue of the belemnoid guard as attempted by Naef' (Jeletzky 1966, p. 62).

EXPLANATION OF PLATE 8

Figs 1–4. *Naefia kabanovi* sp. nov.; Upper Aptian, River Hokodz, north-western Caucasus. 1, 3871/126; dorsal attachment scar. 2, enlarged detail of Fig. 1 showing numerous tiny pores. 3–4, 3871/125. 3, dorsal mural part of septum, covered by inner portion of shell wall, 4, septal neck, showing adorally directed rim on the dorsal side; inner surface of the septal neck is lined by the connecting ring. Scale bars represent 0.1 mm.



DOGUZHAeva, *Naefia*

However, Dauphin concluded that the microstructural analyses of the shell 'do not show fundamental differences in the rostral organization of Mesozoic belemnitids and Cenozoic sepiids' (Dauphin 1985a, p. 70). She assumed that the lamellar layer of the dorsal shield in sepiids represents a modified nacreous layer of the shell of the phragmocone in aulacocerids and belemnitids. This means that sepiids, aulacocerids and belemnitids have broadly the same three layers (inner prismatic, nacreous and outer prismatic) as in the shell wall of ectocochleates (Dauphin 1985a).

The caecum and prosiphon observed in *Spirula* and *Groenlandibelus* are expected to be the characteristic features of the whole order Sepiida (Jeletzky 1966). Jeletzky assumed that Sepiida evolved from ancestors possessing orthoconic phragmocones, shallow lobate sutures, and both the caecum and the prosiphon within the protoconch. Recently, the initial portion of the phragmocone showing the caecum and prosiphon were discovered in the Danian sepoid *Ceratisepia* and the Eocene *Belosepia* (Meyer 1993). This confirms the assumptions that both caecum and prosiphon are diagnostic of Sepiida *sensu* Jeletzky. On the other hand, Meyer (1993) did not attach importance to the differences in protoconch structure, but shared Naef's opinion that sepiids derived from forms which were similar to *Conoteuthis*. He assigned Groenlandibelidae to Diplobelina. However, as Jeletzky (1966) convincingly showed, groenlandibelids differ from diplobelins in possessing a caecum and prosiphon.

Thus, the Aptian coleoids *Adygeya adygensis* and *Naefia kabanovi* seem to confirm that Mesozoic precursors of the Tertiary Sepiida and the Late Cretaceous Groenlandibelidae must have been similar to *Groenlandibelus* and *Naefia*. Recent *Spirula* inherited a shell wall structure which is close to that of *Adygeya*, and a siphuncular structure similar to that of *Naefia*. Comparative studies of *Adygeya*, *Naefia* and *Spirula* demonstrate that spirulids possessed a special kind of internal shell which could hardly be derived from that of the belemnites.

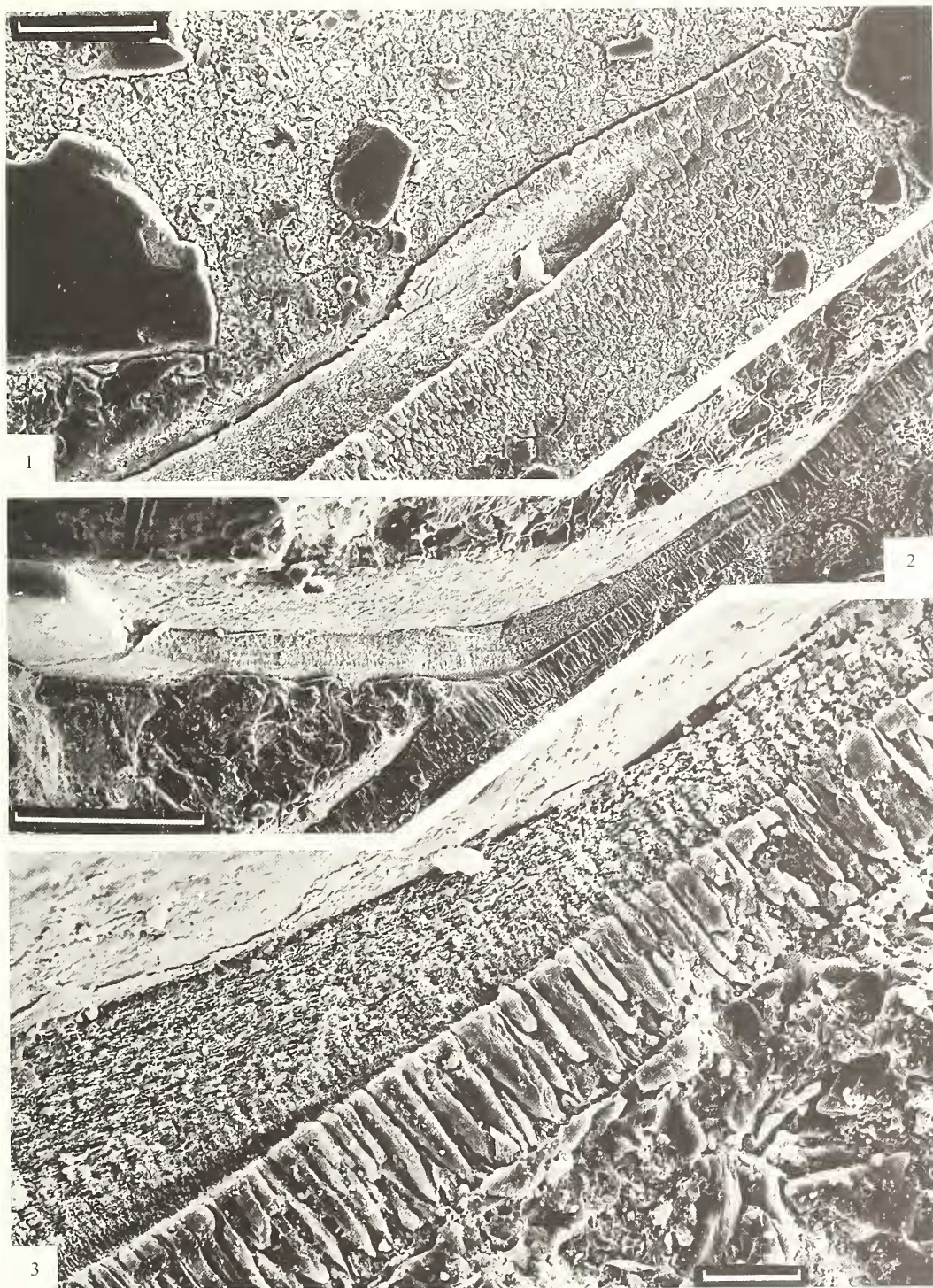
The material studied has led to the conclusion that in the superorder Decabanchia of Doyle *et al.* (1994), which includes *Adygeya*, *Naefia*, *Groenlandibelus*, *Actinosepia*, *Spirula*, *Sepia*, *Belosepia*, *Vasseuria*, *Beloptera* and *Belopterina*, the nacreous layer is absent from the shell wall, whereas in the superorder Belemnoida (Doyle *et al.* 1994), including Aulacocerida (Bandel 1985; Dauphin 1985a), Belemnitida (Barskov 1972-73; Dauphin 1985a) and Diplobelida (unpublished data), it is present. Taking into consideration the high stability of the shell wall structure in cephalopods, I suggest that this difference indicates an early divergence of the two superorders.

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EXPLANATION OF PLATE 9

Figs 1-3. *Naefia kabanovi* sp. nov.; 3871/124; Upper Aptian, River Hokodz, north-western Caucasus. 1, apertural margin on the dorsal side of fully grown shell, showing that the main portion of the shell wall formed a flap around the mural part of the last septum; scale bar represents 100 μm . 2, contact between septum and shell wall; scale bar represents 30 μm . 3, enlarged detail of fig. 2 to show: (a) nacreous structure of the mural part of a septum with well-developed nacreous tablets; (b) organic membrane on the adoral surface of septum; (c) simple prismatic structure of the shell wall on the dorsal side; (d) nearly equal thickness of the septum and shell wall; and (e) distinct boundary between shell wall and septum; scale bar represents 30 μm .



DOGUZHAeva, *Naefia*

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